Estuaries and Coasts (2010) 33:182–194
DOI 10.1007/s12237-009-9235-z

Macrozooplankton Community Dynamics in Relation to Environmental Variables in Willapa Bay, Washington, USA

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Received: 16 July 2008 / Revised: 1 October 2009 / Accepted: 6 November 2009 / Published online: 8 December 2009

Abstract Willapa Bay is a large, economically and ecologically important estuary on the Washington coast, USA for which the zooplankton community has not previously been studied. Thus, in 2006 and 2007, six stations within Willapa Bay were sampled biweekly for macrozooplankton, chlorophyll, and various abiotic variables to elucidate the processes underlying community composition and dynamics. Non-metric multidimensional scaling identified water temperature and upwelling values as major factors defining two distinct temporal communities. High densities and a community dominated by oceanic species (*Calanus pacificus*, *Centropages abdominalis*) marked the winter season, while summer (or the upwelling season) was dominated by estuarine species (Palaemonidae, *Clevelandia ios*). Smaller scale changes in the community were characterized by variation in chlorophyll *a* concentration and salinity and were marked by the presence of other taxa (*Neotrypaea californiensis*, Mysidae). These results point to the importance of physical processes, including the import of marine organisms and retention of estuarine organisms, in the structuring of the macrozooplankton community in Willapa Bay.

Keywords Macrozooplankton · Community structure · Multivariate community analysis · Ordination · Estuary · Washington coast

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Introduction

Estuaries are complex ecosystems characterized by rapidly fluctuating conditions where inputs from both river freshwater and oceanic coastal water can alter the environment as often as every tidal cycle. Although the environment of estuaries can be stressful to organisms due to the large fluctuations in water conditions, organisms that can tolerate such changes thrive because of high productivity levels created by enriched nutrient concentrations (Correll 1978; Cole and Cloern 1987; Howarth 1988). Macrozooplankton, classified in this study by a size larger than 500 μm, are intermediate consumers found in most productive aquatic ecosystems. This group consists of both holoplanktonic and meroplanktonic taxa that consume a large proportion of primary productivity and act as intermediaries between primary producers and higher trophic levels (Gewant and Bollens 2005). This productivity is an important resource for many fish species that utilize these rich systems during larval and juvenile stages when food availability is paramount to survival (Gunderson et al. 1990; Houde and Rutherford 1993; Beck et al. 2001).

In estuaries around the world plankton communities have been found to correlate with various abiotic factors. In a study of several estuaries on the coast of Texas (USA), Holt and Strawn (1983) found that significant differences in macrozooplankton community composition between warm and cool seasons were distinguished by salinity, due to river flow, and temperature. Soetaert and Van Rijswijk (1993) observed that salinity explained most of the variance within a mesozooplankton community, while temperature played a much lesser role in the estuarine reaches of the Schelde River (Belgium and the Netherlands). The macrozooplankton and micronekton community composition in San Francisco Bay (USA) was correlated with season and proximity to the mouth of the estuary (Gewant and Bollens

2005). Season, as defined by temperature, also played a major role in describing two distinct mesozooplankton communities in a Southern California estuary (USA) (Elliott and Kaufmann 2007).

Willapa Bay, an estuary on the southern coast of Washington state (USA), is part of a network of estuaries along the west coast of North America connected through coastal hydrographic processes (Emmett et al. 2000). In Willapa Bay, where more than half of the surface area and volume of the estuary are drained at low tide (Hickey and Banas 2003), conditions may be highly influenced by coastal processes due to the large exchange of water with the coastal ocean. Other inputs to Willapa Bay include the Willapa and Naselle rivers which drain largely undeveloped watersheds, a rarity in coastal systems (Secord and Cohen 2001). Although the relatively small drainage may provide some input into the system, the effect of this input may be superceded by the large tidal influence (Banas et al. 2004).

The California Current System drives the coastal oceans of the eastern Pacific; during the spring and summer it is dominated by the southward California Current, while the northward Davidson Current prevails during the fall and winter (reviewed in Emmett et al. 2000; Hickey and Banas 2003). Coastal upwelling and downwelling events occur annually prevailing during the summer and winter, respectively (Hickey 1989). In the summer, northerly winds favor upwelling which brings colder, more saline, and nutrient-enriched water as close as a few kilometers from shore; during the winter, winds from the south generate downwelling conditions that force warmer, less saline, and nutrient-reduced water onshore (Hickey and Banas 2003; Banas et al. 2004). In Oregon and Washington, these southerly winds also force the Columbia River plume back onshore at which point it can enter Willapa Bay (Roegner et al. 2002; Hickey and Banas 2003; Banas et al. 2004).

Willapa Bay supports commercial fisheries for Dungeness crab (*Cancer magister*), English sole (*Parophrys vetulus*), and the Pacific oyster (*Crassostrea gigas*). The oyster fishery is a large source of income to the region and produces between 10% and 25% of the commercially harvested oysters in the USA (Emmett et al. 2000; Feldman et al. 2000; Ruesink et al. 2006). The oyster fishery is facing major changes in its pest management procedures as new regulations are forcing the fishery to phase out the use of carbaryl (1-napthol n-methylcarbamate) in its management of burrowing shrimp (Pulkkinen 2003). These endemic pests, the ghost shrimp *Neotrypaea californiensis* and the mud shrimp *Upogebia pugettensis*, burrow into the substrate, compromise the sediment stability, and allow oysters to sink and suffocate (Feldman et al. 2000; Dumbauld et al. 2001). Without a viable alternative for pest control, the oyster fishery may suffer, causing regional economic problems and decreasing national oyster supply.

Because Willapa Bay plays a major role in both the economic and ecologic health of the region, it is imperative to document its current biological status. Due to biological invasions (Bollens et al. 2002; Wonham and Carlton 2005; Ruesink et al. 2006), aquaculture activity (Simenstad and Fresh 1995; Ruesink et al. 2006), and pesticide use (Dumbauld and Wyllie-Echeverria 2003; Pulkkinen 2003), the estuary is changing. Macrozooplankton are sensitive to changes in many abiotic factors, natural or anthropogenic (Holt and Strawn 1983; Soetaert and Van Rijswijk 1993; Gewant and Bollens 2005), and therefore the community is a good candidate to analyze in conjunction with variation in environmental conditions. Currently, no studies have examined the macrozooplankton community in Willapa Bay. For these reasons, the current status of Willapa Bay, its plankton community, and the mechanisms affecting their dynamics are important to understand.

This study examined the macrozooplankton community of Willapa Bay with two objectives. The first was to measure the composition, distribution, and concentration of macrozooplankton in Willapa Bay over two consecutive years. The second objective was to correlate community variations to biotic and abiotic factors, including chlorophyll *a* (chl-a) concentration, other community members, salinity, temperature, upwelling indices, and tidal fluctuations. The larger goal was to elucidate the relationships between species and their environment within Willapa Bay as well as to provide insights into estuarine zooplankton dynamics more generally.

Materials and Methods

Study Site

Willapa Bay is a shallow estuary located between the mouth of the Columbia River to the south and Grays Harbor to the north (Fig. 1). The drowned river valley drains a relatively small watershed of 2,900 km^2 (Emmett et al. 2000; Hickey and Banas 2003) and has an area of nearly 350 km^2, half of which is intertidal (Roegner et al. 2002). The estuary is aligned along a north–south axis and is connected to the ocean by a relatively small opening in the northwest corner. One major channel runs south from the mouth connecting with the Naselle River, while another runs east from the mouth to the Willapa River (Banas et al. 2004). Tidal speed and influence vary over the length and width of the estuary and over the tidal cycle (Banas et al. 2004).

Field Sampling

We selected six sampling stations within Willapa Bay (Fig. 1) to cover the spatial extent of the bay and both major

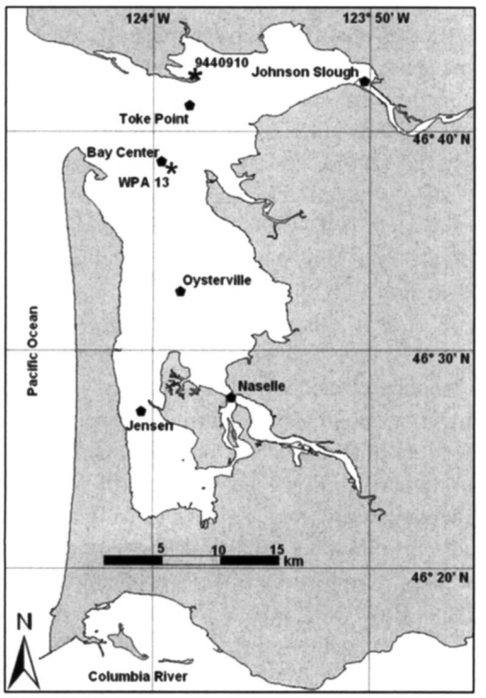

Fig. 1 Map of Willapa Bay, Washington, USA. *Pentagon symbols* denote sampling stations for this study: Bay Center, Oysterville, Toke Point, Johnson Slough, Jensen, Naselle. *Asterisk symbols* denote stations recording daily data: WPA 13 WA DOE mooring for daily temperature, salinity, chl-a, 9440910 NOAA mooring for tides

river channels, in addition to proximity to State of Washington Department of Ecology (WA DOE) monitoring buoys. We sampled January 2006 through December 2007 on a biweekly schedule, corresponding with neap tides. The number of stations sampled varied due to weather conditions and accessibility, but all sampling occurred between 10 A.M. and 4 P.M. and was completed independently of the daily tidal cycle. At each station, samples for macrozooplankton and chlorophyll were collected and environmental conditions recorded.

Macrozooplankton was collected using a 500-μm mesh, 1-m diameter hoop net deployed from a passively moving vessel to approximately 2 m above the bottom and vertically hoisted at a rate of 10–15 m min^{-1}. The net was equipped with a General Oceanics 2030 Flowmeter outfitted with a low-speed rotor. Samples were preserved onboard in 10% buffered formalin. In the laboratory, all specimens in each sample were identified and enumerated to the most specific possible taxonomic classification.

Surface water was collected using a bucket, and 100 mL was filtered onboard onto Whatman 47-mm glass fiber filters and frozen for chl-a analysis via fluorometry (Holm-Hansen and Riemann 1978) using a Turner Designs 10-AU fluorometer.

Water column profiles of temperature, salinity, and dissolved oxygen were collected at each station using a SBE25 Sealogger CTD. CTD data were processed and averaged into 1-m bins (SeaTerm Software), and then water column averages were calculated. Average daily temperature, salinity, and chl-a measurements were compiled from the WA DOE mooring station at Bay Center (WPA 13, Fig. 1; http://www.ecy.wa.gov/programs/eap/mar_wat/moorings_what.html). Meteorological conditions and tidal times and height were collected from the National Oceanic and Atmospheric Administration's (NOAA) Tides and Currents database (http://tidesandcurrents.noaa.gov) for the Toke Point Station (9440910, Fig.1). River flow data were obtained from the US Geological Survey for the Willapa and Naselle Rivers (http://waterdata.usgs.gov/WA/nwis/current/?type=flow).

In addition to environmental variables collected in the bay, we also compiled data on coastal processes and indices. Daily coastal upwelling index values for 45° N were collected from NOAA's Pacific Fisheries Environmental Laboratory (www.pfeg.noaa.gov). These provide an index of the strength of wind forcing on the ocean based on Ekman's theory of mass transport due to wind stress. In addition to sampling date values, we averaged daily values over 7, 15, 30, and 60 days prior to sampling dates. Another metric of upwelling is cumulative wind stress, which represents the energy input to the system over the course of the upwelling season. These data were obtained from S.D. Pierce's web site (http://damp.coas.oregonstate.edu/windstress/), and values corresponding to our sampling dates were included in the analysis.

We also obtained monthly values for the multivariate El Niño/Southern Oscillation index from NOAA's Earth Systems Research Laboratory (www.cdc.noaa.gov/people/klaus.wolter/MEI/mei.html) and the Pacific Decadal Oscillation from the Joint Institute for the Study of Atmosphere and Ocean (http://jisao.washington.edu/pdo/). These indices are based on oceanographic measurements and the appropriate comparison of these to estuarine processes can vary; therefore, the data were lagged between 0 and 6 months.

Spring and fall transition dates for the California Current System were collected from University of Washington's Columbia Basin Research web site (http://www.cbr.washington.edu/data/trans_data.html). Two sets of transition dates were obtained: the biological transition dates that are based on the arrival or disappearance of cold water copepods (Peterson et al. 2006) and the physical transition dates that are determined by a 10-day directional switch in upwelling and sea level (Logerwell et al. 2003).

Statistical Analyses

Macrozooplankton counts were converted to concentration (individuals per cubic meter). Rare species, defined as those found in less than 3% of the samples, are reported but not

included in the statistical analyses. All data were $\log_{10}(x+1)$ transformed. Kruskal–Wallis (χ^2), a nonparametric analysis of variance (Zar 1999), was used to explore spatial variation in individual variables collected as part of the shipboard sampling in Willapa Bay, including total zooplankton abundance, temperature, salinity, chl-a, and specific zooplankton taxa using SAS v 9.1 for Windows.

Nonmetric multidimensional scaling (NMDS) ordination was used to examine relationships between the zooplankton community and all environmental characteristics, both collected and compiled (Clarke and Ainsworth 1993; McCune and Grace 2002). Sorenson's (Bray–Curtis) distance measure was used, and the ordination that most adequately described the data was chosen based on the final stress (a measure of the goodness-of-fit between the data and the final ordination) in relation to the dimensionality (Kruskall and Wish 1978). Pearson correlation coefficients (r) were used to evaluate the relationships between the ordination axes and environmental variables.

Indicator species analysis (ISA) determined which taxa had the strongest affiliations to each categorical variable included in the analysis (day, month, year, station, and season). This technique evaluates each species against a perfect indicator that would faithfully and exclusively occur in a particular group; each species is assigned an indicator value for each group based on the degree of faithfulness and exclusiveness (Dufrêne and Legendre 1997). Indicator values were determined statistically significant via Monte Carlo randomization. All multivariate analyses were conducted in PC-ORD for Windows 5.10 (McCune and Mefford 1999). To determine which environmental variables were correlated with individual species, a posteriori Spearman rank correlation coefficients (r) were calculated between the dominant environmental variables and indicator species (SAS v 9.1).

Results

Macrozooplankton Concentration

A total of 35,468 individuals representing 75 taxa were identified in 184 samples collected over 41 cruises between January 2006 and December 2007 (Table 1). Total zooplankton density varied between the 2 years, although not significantly ($\chi^2=0.33$, $p=0.57$). The spring peak in March was twice as high in 2006 than in 2007 (Fig. 2a). Densities in June and July of 2006 were much lower than those seen in 2007. Finally, the autumn and winter densities in 2007 were higher than in 2006.

Total macrozooplankton concentration varied spatially ($\chi^2=18.17$, $p<0.01$). In general, stations closer to the mouth supported higher densities than stations farther upestuary, with a trend of decreasing density as distance from the mouth increased. The largest differences in density between upper and lower stations were found during months with peak concentrations (Fig. 2a). Upper and lower estuary stations were classified based on water retention times; the upper estuary stations (Jensen and Naselle, Fig. 1) have been shown to have higher water retention times than all other stations (Banas and Hickey 2005; Banas et al. 2007).

Hydrography and Chlorophyll *a*

Water temperatures recorded during sample collection varied by more than 10°C between winter lows and summer highs. The coldest months of February and March had temperatures close to 6°C, while July and August, the warmest months, had temperatures up to 19°C (Fig. 2b). The magnitude and timing of the changes in temperature were similar between 2006 and 2007 ($\chi^2=0.67$, $p=0.41$). There were no spatial differences in average water column temperatures among the stations ($\chi^2=3.88$, $p=0.57$), although more variation was seen between lower and upper estuary stations during the summer months (Fig. 2b).

The temporal pattern in salinity was less clear, ranging from below 10 in early January 2007 to over 30 on several dates during the summer months of 2006 (Fig. 2c). Overall, 2007 had lower salinities than 2006 ($\chi^2=12.12$, $p<0.01$). There was also spatial variation in salinity among the stations ($\chi^2=31.33$, $p<0.01$), showing a trend of decreasing salinity as distance from the mouth increased. The difference in salinity between upper and lower estuary stations was fairly consistent throughout the sampling period (Fig. 2c).

Variation was high in chl-a concentrations collected with zooplankton samples, particularly on dates with peak measurements (Fig. 2d). However, seasonal trends captured during sampling were consistent with trends recorded at the WA DOE mooring station. Overall, 2007 had significantly lower chl-a than 2006 ($\chi^2=15.78$, $p<0.01$). Spatially, higher concentrations were found at stations closer to the mouth of the bay ($\chi^2=31.07$, $p<0.01$), with the highest chl-a occurring in the Willapa River channel stations (Toke Point and Johnson Slough, Fig. 1).

The intrusion of water from the Columbia River plume has been documented in Willapa Bay (Roegner et al. 2002). This process has the potential to quickly change the characteristics of the water within the bay. Water from the Columbia River plume generally has a salinity of 22, temperatures between 14°C and 16°C, and low fluorescence (Roegner et al. 2002; Morgan et al. 2005). Data from the WA DOE mooring station were reviewed to determine if our sampling dates coincided with a plume intrusion event. None of the sampling dates were found to have all

Table 1 List of macrozooplankton species identified during the study ranked in terms of total numbers[a]

Taxon	Number of samples	Total number	Percentage
Calanus pacificus	86	10,500	29.6
Centropages abdominalis	123	7,836	22.1
Neotrypaea californiensis	96	2,904	8.19
Pinnotheridae	128	2,085	5.88
Mysidae	58	2,076	5.85
Hydrozoa	74	2,021	5.70
Crangon spp.	77	1,379	3.89
Cumella vulgaris	70	1,224	3.45
Amphipod	70	705	1.99
Syllidae	86	488	1.38
Lamprops quadriplicata	59	443	1.25
Podon sp.	38	393	1.11
Pseudocalanus sp.	54	370	1.04
Bivalve larvae	37	354	1.00
Hippolytidae	64	264	0.74
Epilabidocera longipedata	52	238	0.67
Clevelandia ios	38	210	0.59
Barnacle nauplii	28	206	0.58
Acartia spp.	41	202	0.57
Eurytemora americana	19	189	0.53
Daphnia sp.	17	169	0.48
Palaemonidae	26	156	0.44
Paguridae	12	147	0.41
Tortanus discaudatus	34	136	0.38
Caprella sp.	60	127	0.36
Sagitta sp.	29	84	0.24
Majidae	19	56	0.16
Lithodidae	24	51	0.14
Nippoleucon hinumensis	30	45	0.13
Osmeridae	18	45	0.13
Leptocottus armatus	21	36	0.10
Eucalanus sp.	5	27	0.08
Xanthidae	8	22	0.06
Grapsidae	8	19	0.05
Larval fish	8	16	0.05
Cancer sp.	8	16	0.05
Oithona sp.	5	16	0.05
Clausidium vancouvereas	11	15	0.04
Barnacle cyprid	6	14	0.04
Hemicyclops sp.	8	12	0.03
Isopod	8	11	0.03
Porcellanidae	5	9	0.03
Pleuronectes isolepis	5	6	0.02
Total collected	184	35,468	100.00

Number of samples = number of samples in which taxon was present, total number = number collected, percentage = percent of total catch

[a] Taxa that were found in less than 3% of the samples and not included in statistical analyses: *Armandia brevis*, calanoid copepod, *Cancer* sp. megalope, caridean, copepod, crab zoea, Ctenophora, cumacean, cyclopoid copepod, decapod megalope, Diogenidae, ephyra, *Errex zachirus*, *Evadne* sp., fish, harpacticoid copepod, Hemigrapsidae, Hippidae, Liparidinae, *Macropsis* sp., megalope, *Mesolamprops* sp., Ostracod, Pandalidae, *Parophrys vetulus*, *Platichthys stellatus*, polychaete, sea lice, shrimp, snail, *Synghathus leptorhynchus*, *Temora* sp.

three defining characteristics; therefore, we do not believe we sampled during a plume intrusion event.

The transition dates for the California Current System varied between the years. In 2007, both the spring and fall transition dates were a month earlier than in 2006. In 2006, the upwelling season began on April 22nd and prevailed through October 31st as determined by a 10-day directional switch in upwelling (Logerwell et al. 2003), while in 2007,

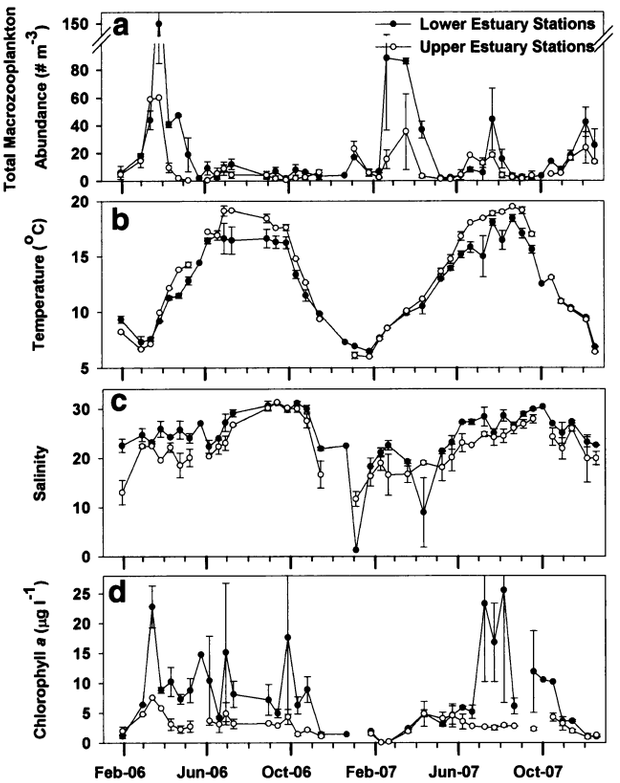

Fig. 2 Regional means (±SE) of total macrozooplankton abundance (no. per cubic meter) (**a**) and water column means (±SE) for temperature (**b**), salinity (**c**), and chlorophyll *a* (**d**) in Willapa Bay, 2006–2007. *Closed symbols* denote means at lower estuary stations (Bay Center, Oysterville, Toke Point and Johnson Slough); *open symbols* denote means at upper estuary stations (Jensen and Naselle)

upwelling conditions began earlier, starting on March 15th and continued only through September 27th.

Macrozooplankton Community Analysis

NMDS, a multivariate ordination technique, of the zooplankton samples resulted in a three-dimensional solution, with a final stress of 18.07 after 235 iterations, explaining 73.0% of the variance in the macrozooplankton community (Fig. 3). While this is considered a "fair" level of stress, the large number of sample units partly explains the high value and justifies continued analysis (Kruskall and Wish 1978; McCune and Grace 2002). The solution was found to be statistically different from a randomized solution using a Monte Carlo test (p=0.01).

Axis 1 explained 29.1% of the total variation. The environmental variables most strongly correlated to this axis were temperature (Pearson's r=0.817), upwelling season as described by physical characteristics (Logerwell et al. 2003; r=−0.731), and the species richness (number of species) of each sample (r=−0.697). Axis 2 explained 23.5% of the variability and was most strongly correlated with species diversity; because this variable was more strongly correlated with axis 1, axis 2 was not evaluated further. Axis 3 explained 20.4% of the variation (Fig. 3) and was correlated with chlorophyll *a*, salinity (both collected in conjunction with zooplankton samples), and distance from the mouth of the bay (chl-a: r=−0.427, salinity: r=−0.420, distance: r=0.418).

Axis 1 was strongly correlated with the upwelling season variable which classified all samples into one of two categories: those collected during the upwelling (summer) season or those that were not (winter). Using this variable to code the array of samples in the NMDS plot, the separation of symbols shows the strong correlation of sample community composition to upwelling season (open versus closed symbols, Fig. 3). Temperature, the strongest quantitative correlate on this axis, was positively correlated; a difference of more than 6°C was found between the average water temperatures between the seasons (Table 2). This axis was also strongly correlated with species richness; this variable was negatively correlated, indicating that samples collected in the colder months had higher species richness (Fig. 3 and Table 2).

The variation in axis 3 was correlated to chl-a, salinity, and location. Chl-a and salinity were negatively correlated

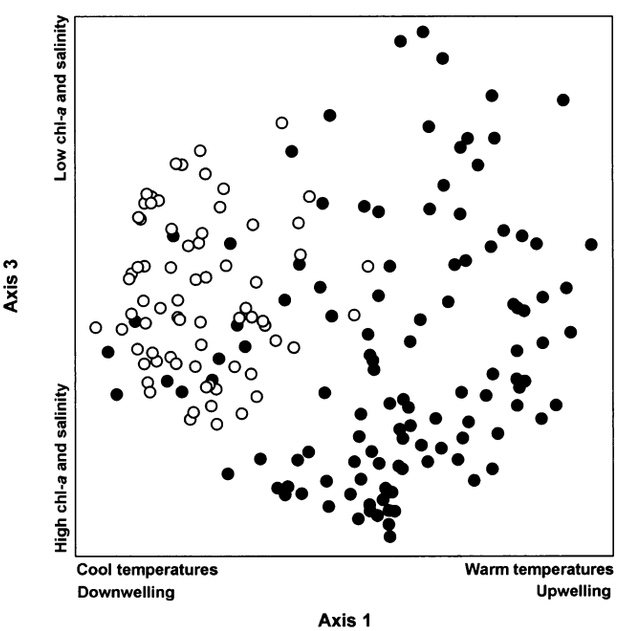

Fig. 3 Non-metric multidimensional scaling ordination of the 184 samples collected during the study. *Open symbols* indicate samples collected during the winter season and *closed symbols* indicated samples collected during the summer (upwelling) season as described by Logerwell et al. (2003). Axis 1 (r^2=0.291) is associated with temperature (r=0.817) and physical upwelling season (r=−0.731). Axis 3 (r^2=0.204) is associated with chlorophyll *a* concentration (r=−0.427) and salinity (r=−0.420)

Table 2 Mean values (±SE) for major environmental variables for both seasons

	Physical season	
	Winter	Summer (upwelling)
Temperature (°C)	8.91 (0.23)	15.60 (0.25)
Species richness	12.39 (0.55)	7.00 (0.42)
30-day Upwelling	−49.05 (4.44)	30.31 (2.12)
Cumulative upwelling	0 (0)	−2.27 (0.16)
7-day River discharge (ft^3/s)	866.18 (100.45)	135.80 (18.94)
Chlorophyll a (μg/L)	3.90 (0.62)	6.92 (0.97)
Salinity	21.55 (0.59)	25.71 (0.45)
Distance from the mouth (km)	17.87 (0.99)	17.55 (0.78)

with axis 3, while distance from the mouth of the bay was positively associated. Therefore, samples with higher chl-a concentrations and salinities were collected closer to the mouth of the bay. Chl-a concentrations were considerably higher in the summer months, whereas the salinity of both seasons was well within estuarine levels (Table 2).

ISA was used to identify which of the 43 species included in the ordination were indicative of the seasons. 23 of the 27 species abundant enough to be statistically significant indicators were found to have strong indicator values for season (Table 3). The winter season was identified most strongly by the presence of two calanoid copepods, *Calanus pacificus* and *Centropages abdominalis*, and the mysid shrimp family, Mysidae. The summer (upwelling) season was identified by the presence of two larval decapods, *N. californiensis* and species of the Palaemonidae family, and a larval fish, *Clevelandia ios*.

Density Patterns and Environmental Associations of Individual Taxa

Two of the species indicative of the cold season (*C. pacificus*, *C. abdominalis*) had major peaks in March of both years in addition to elevated abundances in other winter months (Fig. 4a, b). *C. pacificus* was mostly absent from the plankton during summer months; however, *C. abdominalis* was seen in low abundances sporadically throughout the year. Both *C. pacificus* and *C. abdominalis* were highly correlated with all the environmental variables associated with axis 1 and most strongly associated with the 30-day upwelling average (Table 4). On axis 3, *C. pacificus* was most strongly associated with salinity, and *C. abdominalis* was not associated with any of the variables. Mysidae was found in high abundance in the winter months of both years, with peak densities occurring in January 2007 (Fig. 4c). This family was strongly correlated with all of the environmental variables associated with both axes (Table 4). The strongest relationships for each axis, both negative, were with temperature and salinity.

The strongest indicator of the upwelling season, *N. californiensis*, had increased abundances in the spring and sustained elevated abundances through September (Fig. 5a). *N. californiensis* was most strongly associated

Table 3 Indicator values (IV) for taxa with significant Monte Carlo p values ($p<0.05$) for seasons defined by the physical upwelling factor

	Indicator values	
	Winter	Summer
Winter season species		
Acartia spp.	**40**	1
Amphipod	**45**	6
Barnacle nauplii	**21**	2
Calanus pacificus	**84**	2
Centropages abdominalis	**68**	13
Crangon spp.	**51**	6
Cumella vulgaris	**46**	6
Epilabidocera longipedata	**34**	3
Eucalanus sp.	**6**	0
Eurytemora americana	**13**	1
Hydrozoa	**44**	7
Mysidae	**68**	0
Osmeridae	**18**	0
Paguridae	**10**	0
Pleuronectes isolepis	**7**	0
Podon sp.	**21**	3
Porcellanidae	**5**	0
Pseudocalanus sp.	**42**	3
Sagitta sp.	**26**	1
Tortanus discaudatus	**35**	0
Summer (upwelling) season species		
Clevelandia ios	0	**31**
Neotrypaea californiensis	7	**51**
Palaemonidae	1	**17**

Bold indicates a good IV for the cluster (IV>5× higher than that for the other group)

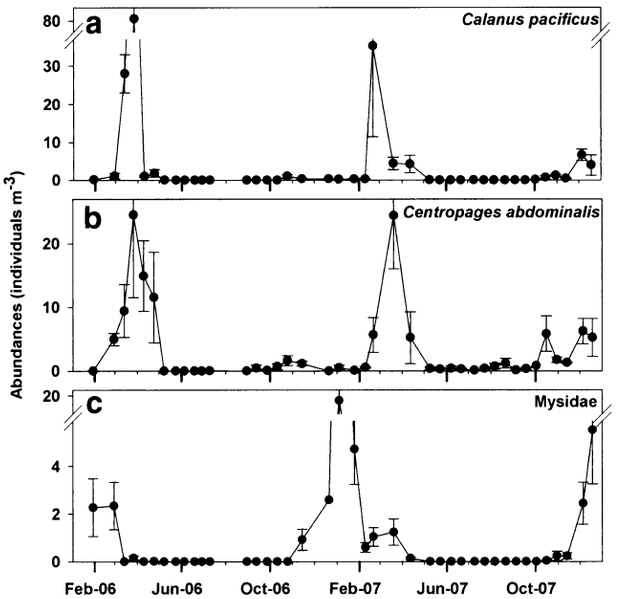

Fig. 4 Bay-wide mean (±SE) abundances (no. per cubic meter) of *C. pacificus* (**a**), *C. abdominalis* (**b**), and Mysidae (**c**) in Willapa Bay, 2006–2007

with temperature on axis 1 and chl-a on axis 3 (Table 4). Two other taxa associated with the warm season, *C. ios* and Palaemonidae, were not found in the plankton in winter months and increased in abundance during summer months (Fig. 5b, c). Both taxa were highly related to all the variables on axis 1 and most strongly correlated with temperature (Table 4). On axis 3, *C. ios* was positively associated with distance from the mouth of the bay, and Palaemonidae was not associated with any of the variables.

Discussion

Zooplankton, Chlorophyll *a*, and Hydrography: Yearly Trends

Seasonal peaks in zooplankton are common in temperate estuaries as conditions become optimal; temperatures rise as light increases, generating more primary productivity, which supports larger populations of consumers. The range of total density observed in Willapa Bay (0–150 individuals per cubic meter) was lower than other locations where a similar size class was sampled (e.g., 0–400 individuals per cubic meter by Champalbert et al. 2007; 400–600 individuals per cubic meter by Duggan et al. 2008), though no other study in a temperate estuary could be found that looked at exactly the same size class (>500 μm). The peaks in zooplankton density were due to large increases in marine pelagic copepods; a similar marine influence has been recorded in other estuaries, including the Senegal River estuary (Champalbert et al. 2007).

Several zooplankton taxa had significantly higher densities in 2007 than 2006 (*C. abdominalis*, Mysidae, *C. ios*, Palaemonidae). The differences in abundance might be explained by variation in the beginning of the upwelling season. The timing of upwelling initiation has been linked to system productivity; earlier upwelling initiation generates greater productivity (Peterson et al. 2006), and in fact, the 2007 upwelling season began 1 month earlier than in 2006.

The yearly range and pattern of temperature and salinity measured during zooplankton sampling were similar to other US west coast estuaries (Frolander et al. 1973; Gewant and Bollens 2005). Although temperature did not vary between the 2 years, 2006 had higher overall salinities

Table 4 Spearman rank correlation coefficients for major environmental variables for the ordination axes and indicator species for the primary and secondary groups

	Axis 1				Axis 3		
	Temperature	30-day Upwelling	Cumulative upwelling	7-day Discharge	Chl *a*	Salinity	Distance to mouth of bay
Winter species							
C. pacificus	−0.7649**	**−0.7864****	0.7481**	0.7651**	−0.1754*	**−0.3989****	−0.0311
C. abdominalis	−0.5394**	**−0.6132****	0.5068**	0.5027**	−0.0075	−0.1271	−0.1077
Mysidae	**−0.7488****	−0.6555**	0.6756**	0.6846**	−0.5555**	**−0.5824****	0.1663*
Summer (upwelling) species							
N. californiensis	**0.2993****	0.1480*	−0.1334	−0.1247	**0.3903****	0.1380	−0.3323**
C. ios	**0.4296****	0.3768**	−0.2054**	−0.2405**	0.0184	0.0008	**0.2449****
Palaemonidae	**0.2970****	0.2417**	−0.2210**	−0.2377**	0.0258	0.0920	0.1394

Bold indicates the highest correlated variable for each species on each axis

*$p<0.05$; **$p<0.01$

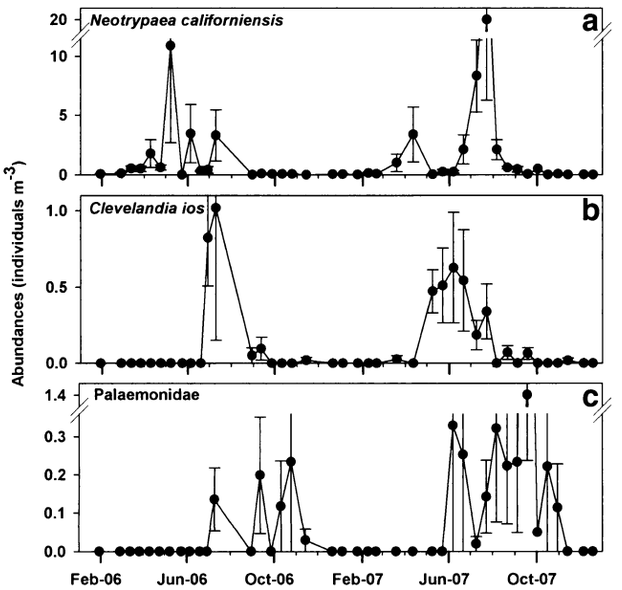

Fig. 5 Bay-wide mean (±SE) abundances (no. per cubic meter) of *N. californiensis* (**a**), *C. ios* (**b**), and Palaemonidae (**c**) in Willapa Bay, 2006–2007

than 2007. This could have been a result of higher river discharge in early 2007 (waterdata.usgs.gov).

Primary Source of Variation: Seasonality

The importance of coastal oceanography to phytoplankton biomass in Pacific Northwest estuaries has been studied previously (Roegner et al. 2002; Hickey and Banas 2003; Newton and Horner 2003; Banas et al. 2007). It is therefore not surprising that we found coastal upwelling to be an important environmental correlate to the community composition of macrozooplankton in Willapa Bay. The winter season (October–April) was distinguished by negative upwelling values (downwelling conditions), a northward flowing coastal current, cold water, species-rich samples, and high macrozooplankton densities (Table 2). Conversely, warm water temperatures, higher chl-a and salinity, and lower species richness and macrozooplankton densities categorized the summer (upwelling) season. Season has been found to be an important indicator of community composition in other systems; temperature and salinity are frequently the defining characteristics for categorizing plankton communities (Holt and Strawn 1983; Gewant and Bollens 2005; Champalbert et al. 2007).

The samples collected during the winter season consisted predominantly of calanoid copepods, many of which have been found in coastal waters off Oregon and Washington (Frolander et al. 1973; Peterson and Miller 1977; Peterson and Keister 2003). However, two of the copepod species found to co-occur in Willapa Bay (*C. pacificus* and *C. abdominalis*) are members of different coastal regimes. Frolander et al. (1973) observed a similarly mixed winter zooplankton community in Yaquina Bay, an estuary on the coast of Oregon (USA).

C. pacificus, a warm-water species, has been found off the nearshore Oregon coast, primarily during late spring and fall months (Peterson and Keister 2003) and in both on- and offshore environments in June and July (Morgan et al. 2003). Conversely, *C. abdominalis*, a cold-water neritic species, was found over the Oregon continental shelf during the strong upwelling season in the summer months (Keister and Peterson 2003; Morgan et al. 2003). The mixing of taxa indicative of separately occurring communities has been observed off the central Oregon coast where winter communities contained both northern and southern species because the northward extension of the Davidson Current increased the ranges of warm water species (Peterson and Miller 1977). The presence of oceanic species has also been observed in the Columbia River estuary where these species were found in both the pelagic ocean plume and the estuarine mixing zones (Jones et al. 1990).

The different temporal occurrence of certain taxa in the coastal ocean (summer) and Willapa Bay (winter) suggests the movement of organisms from the coast into the bay. One explanation may be primarily biological. During the winter, upwelling is suppressed and the waters of the coastal oceans may be lacking nutrient resources. At the same time, increased river flow into the bay (Table 2) could bring elevated nutrient levels to the area and provide more resources than are available in the coastal ocean. Another reason these coastal taxa are found in the bay may be physical. Onshore winds, characteristic of the downwelling season, force surface water, and organisms within it, onshore and into Willapa Bay. A similar process of onshore transport was documented for phytoplankton (Roegner et al. 2002; Newton and Horner 2003), but ours is the first study to suggest this phenomenon may also be affecting zooplankton in Willapa Bay.

The summer (upwelling) zooplankton community was described by only a few taxa due to high variability and low concentrations. Two of the three indicator species for this season (*C. ios*, Palaemonidae) have both larval and adult stages that reside within the bay. *C. ios* is a small goby that takes refuge in the burrows of other animals, including *N. californiensis* (MacGinitie 1934). These fish spawn during the spring and summer and spend 2–4 weeks as larvae in the water column. We found larval *C. ios* throughout the warm season, with peak densities in June and July. Similarly sized and timed density peaks were recorded in Dabob Bay, Washington (Bollens et al. 1992) and Elkhorn Slough, California (Yoklavich et al. 1992). Both *C. ios* (χ^2=14.07, p=0.02) and Palaemonidae (χ^2=19.93, p<0.01) were found to vary significantly across stations, with highest densities in

the upper estuary (Jensen and Naselle, Fig. 1). This pattern of retention is indicative of estuarine resident species and was similarly recorded for larval and adult *C. ios* in Elkhorn Slough (Yoklavich et al. 1992) and larvae of *Palaemon macrodactylus* in the San Francisco estuary (Gewant and Bollens 2005). Vertical migratory behavior may be one of the reasons more species were not collected as they were not likely to be consistently sampled by the methods of this study because they are often found in close proximity to the bottom (Morgan et al. 1997; Keister and Peterson 2003).

Secondary Sources of Variation: Event-Scale Processes

Willapa Bay is a long and narrow estuary with a small opening at one corner. Along the north–south axis, there is nearly a 20-km difference between our sampling station closest to the mouth of the bay and the one farthest upriver. It is therefore not surprising that hydrological and biological factors vary along the extent of the bay. Previous studies have shown the decreasing influence of the coastal ocean along the major axis of the bay (Roegner et al. 2002; Newton and Horner 2003; Ruesink et al. 2003; Banas et al. 2004, 2007). Most of the variation observed by our study in salinity, chl-a, and total macrozooplankton abundance also occurred along this axis of the bay. With the demonstrated influence of the coastal ocean, it follows that changes in this major source of water and organisms have the potential to alter the zooplankton community within the bay.

The variation in chl-a, salinity, and space were accounted for on axis 3 of the NMDS ordination (Fig. 3). Changes in chl-a and salinity can be influenced by event-scale phenomena (on the order of days to weeks) such as changes in winds, river flow, and coastal upwelling (Banas et al. 2004). These event-scale processes have the potential to influence the community composition of zooplankton more rapidly and for a shorter period than seasonal-scale processes (e.g., upwelling and temperature). Similarly, tidal-scale processes can also alter the zooplankton community; however, our sampling regime was not resolved enough to detect changes on this short a timescale.

Offshore from Willapa Bay, phytoplankton blooms that arise due to active upwelling can be forced into the bay when the upwelling winds relax and water is forced onshore (Roegner et al. 2002). When oceanic primary production is forced into the bay, a gradient of decreasing chl-a with increasing distance to the mouth of the estuary is created (Roegner et al. 2002; Newton and Horner 2003; Banas et al. 2007). Presumably, this event-scale process occurs periodically throughout the upwelling season, suggesting that the peaks in chl-a observed between May and October may be of oceanic origin (Fig. 2d). The inundation of the bay with food-rich waters may stimulate the reproduction of taxa that breed within the bay.

N. californiensis was the strongest indicator species for the summer (upwelling) season (Table 3) and was positively correlated with chl-a (Table 4). Larvae are present in the water column as they move out of the estuary to develop in the nearshore coastal ocean (Johnson and Gonor 1982); after 6–8 weeks, they return to settle in the bay (Dumbauld et al. 1996). Throughout our entire study, we caught only stage I larvae or those individuals presumably exiting the estuary. Adult *N. californiensis* are residents of Willapa Bay that burrow into the sediments. These shrimp produce eggs that hatch between April and August, and females closer to the mouth of the estuary have been found to produce eggs earlier than those farther upriver (Dumbauld et al. 1996). This, combined with the correlation between larvae and chl-a, suggests that the transport of phytoplankton blooms from the coastal ocean into the bay may be an important resource and/or cue for *N. californiensis*.

Similar to changes in chl-a due to oceanic influence, intrusion by the Columbia River plume can occur during the winter season (and storm events) which forces lower salinity, nutrient-poor water into Willapa Bay (Roegner et al. 2002). Though none of the dates sampled had water conditions indicative of this phenomenon (salinity, ~22; temperature, ~14–16°C, low fluorescence; Roegner et al. 2002; Morgan et al. 2005), variation in salinity was recorded between subsequent sampling dates. Changes in the salinity within the bay could indicate the fluctuating and competing influences from both the ocean and the rivers. While Willapa Bay is usually well mixed, high salinity (and occasionally low oxygen) water from offshore can enter the bay and remain at depth (Bollens, unpublished data). However, the overall pattern of salinity within the bay fits the expected relationship of lower salinity during times of peak river outflow and higher salinity during the upwelling season when saltier water is brought to the surface just offshore (Hickey et al. 2002; Banas et al. 2004). A similar seasonal pattern of salinity was documented in Yaquina Bay (Frolander et al. 1973).

The presence of the Mysidae family in the community occurred during the winter season and showed large peaks in abundance December through February (Fig. 4c). The largest peak in January 2007 coincided with a drop in salinity (Fig. 2c) and a large river discharge event (data not shown). Mysids usually reside in the upper reaches of estuaries in low-salinity zones (Dean et al. 2005; Gewant and Bollens 2005); their presence in the lower reaches of the estuary may be due to flushing during large rain events (Baldó et al. 2001). This supports the possibility that the abundance patterns of Mysidae in Willapa Bay might be the result of suboptimal conditions upriver and/or due to transport by increased river flow.

Summary and Conclusions

Our study illustrates the importance of both internal and external processes on estuarine macrozooplankton communities. These insights are important to understanding the specific processes at work within Willapa Bay as well as estuarine zooplankton dynamics in general. In Willapa Bay, the influence of the coastal ocean has been documented in terms of hydrography (Hickey et al. 2002; Banas et al. 2004), primary production (Roegner et al. 2002; Newton and Horner 2003), and secondary production (Ruesink et al. 2003; Banas et al. 2007). Our study further explored the importance of coastal inputs into the bay and how it related to the macrozooplankton community. The findings here corroborate the previous findings that the coastal ocean is a major influence in Willapa Bay, including the import of oceanic species. However, the connectivity between the bay and the coastal systems accounts for only part of the seasonality within the bay.

Estuarine processes and organisms play a large role in the dynamics of the bay during summer months when coastal input is lessened by offshore winds and the zooplankton community contains estuarine-retaining species. The estuarine-based food web of this system is of particular importance as it supports many recreationally and commercially important species (Gunderson et al. 1990). The ability of the macroinvertebrate community to continue to support a wide variety of higher trophic species can be altered by pesticide application or habitat alteration (Simenstad and Fresh 1995). The results of this and other studies show that Willapa Bay continues to support a diverse community of epibenthic organisms despite continued application of herbicides, pesticides, and physical disturbance due to aquaculture (Simenstad and Fresh 1995; Simenstad et al. 1996). What is not clear, however, is if increased aquaculture production (Ruesink et al. 2006) has resulted in reduced production in other assemblages and trophic levels. Nevertheless, based on the similarity of Willapa Bay to other estuaries on the coasts of Oregon and Washington (Hickey and Banas 2003), processes observed here may also be occurring in these neighboring ecosystems.

Our study has produced the first comprehensive analysis of macrozooplankton in Willapa Bay, Washington. This provides important new information regarding the quantity and quality of resources available to higher trophic levels (e.g., fish and birds) and adds to the general knowledge of food web dynamics within Willapa Bay. Additionally, this study documents the presence of planktonic stage I larvae of the ghost shrimp, *N. californiensis*, adults of which are a pest species to the economically important shellfish industry in Willapa Bay.

In summary, we found much of the variation in the macrozooplankton community in Willapa Bay to be correlated with water temperature, chl-a, and salinity. The seasonality in these variables was additionally influenced by the California Current System and the prevailing direction of upwelling winds. Winter communities in Willapa Bay predominantly comprised marine species that are often found in the coastal ocean during other seasons, and summer (upwelling) communities were dominated by estuarine species, including larval stages of decapods and fish, which as adults are residents of the bay. Secondary variation in the macrozooplankton over shorter timescales was related to changes in chl-a and salinity and characterized by responses of individual taxa.

Acknowledgments We thank A. Helms, R. Hooff, J. Quenette, I. McComas, L. Marko, J. Breckenridge, L. Friedenberg, K. Olsen, and J. Duerr for their help in the field, and O. Kalata and L. Marko for assistance with taxonomy. Additionally, thanks go to D. Gewant and R. Hooff for assistance with multivariate techniques, to S. Pierce for providing cumulative upwelling data, and to A. Solow for his generosity in providing access to facilities during the revision process. Finally, thanks go to G. Rollwagen-Bollens, C. Schultz, and B. Tissot for their comments on early versions of the manuscript.

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